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Comparative Study of Temporal Resolution in the Visual Systems of Mesopelagic Crustaceans

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Abstract. The temporal characteristics of the visual systems of eight species of mesopelagic crustaceans were studied using the electroretinogram (ERG). Experiments were conducted on shipboard, using dark-captured specimens collected off the south coast of Cuba. As one would expect based on the relative intensity differences in their light environments, the deepest living species, *Systellaspis debilis* and *Sergia filictum*, have low maximum critical flicker fusion frequencies (CFFs) of 21–25 Hz, whereas the shallower living species *Oplophorus gracilirostris* and *Janicella spinacauda* have higher maximum CFFs (31–32 Hz). One of the shallowest living species, *Funchalia villosa*, has an unusually low maximum CFF (24 Hz), which may be a function of working with a dark-adapted eye. Two of the bilobed euphausiid species, *Nematobrachion flexipes* and *N. sexspinosus*, have very high maximum CFFs (44–57 Hz), comparable to those of surface-dwelling crabs, even though they live between 400 and 600 m. The maximum CFF of *Stylocheiron maximum*, a shallower living bilobed euphausiid, is only 36 Hz, indicating that maximum CFF among the euphausiids cannot be correlated with depth of occurrence. The unusually high flicker fusion frequency of the deeper living euphausiids may be correlated to their preference for bioluminescent prey.

Introduction

Autrum's studies of insect photoreceptors in the 1950s gave rise to the idea that the response dynamics of the retina match the habitat and lifestyle of the organism. In these classic studies, he established that the eyes of rapidly moving day-active species have better temporal resolution, as indicated by flicker fusion frequencies of 200–300 Hz, than the eyes of slower moving night-active forms, with flicker fusion frequencies of 10–20 Hz (Autrum, 1950, 1958; Autrum and Stöcker, 1952). These extracellular studies, using the electroretinogram (ERG), which is the summed mass response from a large number of receptor cells, were later supported by studies on the intracellular responses of single cells (Howard *et al.*, 1984; de Souza and Ventura, 1989). Since the light environment of mesopelagic crustaceans is similar to that of nocturnal insects, one might predict that they would also have fairly low temporal resolution, and that temporal resolution would be correlated with daytime depth of occurrence. Although the spatial resolution, which is a function of the structure and optics of photoreceptors, has been studied in a number of mesopelagic species (see Cronin, 1986; Land, 1990, for review), the temporal resolution, which is a function of the membrane properties of the receptor cells themselves (see Weckström and Laughlin, 1995, for review), has received little attention. As shown by the theoretical analysis of Srinivasan and Bernard (1975), visual acuity is dependent on both the spatial resolution and the temporal resolution of the eye, because for most organisms, visual targets are rarely stationary. Either the organisms themselves are actively moving, so the environment is in motion with respect to their photoreceptors, or their photoreceptors are moving because of muscle tremor or nystagmus. Srinivasan and Bernard (1975) determined that at angular velocities (of the object with respect to the organism viewing it) above a critical value, spatial resolution is more dependent on the temporal properties of the photoreceptor cells than on the structural optics of the eye. Therefore, for any comprehensive analysis of the visual system of an organism, both the spatial and temporal characteristics of the photoreceptor need to be studied.

Studies on temporal resolution in mesopelagic organisms are rare, due to the difficulties in collecting visually competent organisms and keeping them alive during transport back to shore-based labs. The only published study on the temporal characteristics of the visual systems of mesope-

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lagic organisms is by Moeller and Case (1995), in which they demonstrated that two species of deep-sea crustaceans have very low flicker fusion frequencies (8–12 Hz), compared to much higher maximum flicker fusion frequencies (50–60 Hz) for shallow-water crabs (Bröcker, 1935; Crozier and Wolf, 1939). However, Moeller and Case (1995) measured the critical flicker fusion frequency at threshold light intensities, which is difficult to compare between species because (1) the threshold sensitivity of a crustacean eye measured using the ERG technique varies considerably from preparation to preparation (pers. obs.), and (2) critical flicker fusion frequency is dependent upon the intensity of the stimulus light (Bröcker, 1935; Crozier and Wolf, 1939; Crozier *et al.*, 1939). A less problematic characteristic to use for comparative studies of temporal resolution is the *maximum* critical flicker fusion frequency. This is the maximum flicker rate that the eye is capable of following at any light intensity. In the current study, the maximum critical flicker fusion frequencies of the photoreceptors of eight species of mesopelagic crustaceans from a variety of depths (250–900 m) were examined using ERG recordings. The results of these experiments indicate that several species from this dim light environment have surprisingly high maximum flicker fusion rates. These unusually high rates do not appear to be a function of depth of occurrence, but rather, appear to be more closely correlated with the bioluminescence of the preferred prey.

Materials and Methods

Animal collections

The crustacean species used in this study (Table 1) were collected off the south coast of Cuba on a research cruise aboard the RV *Seward Johnson*, with a 2.4 × 1.8 m Tucker trawl fitted with a thermally insulated, light-tight closing collecting container (cod-end). The light-tight cod-end was closed at depth, ensuring that the organisms inside were not exposed to damaging light levels at the surface, as studies have demonstrated that even low levels of light can cause permanent structural and physiological damage to the photoreceptors of light-sensitive species (Loew, 1976; Nilsson and Lindström, 1983; Frank and Case, 1988b). Once at the surface, the cod-end was detached from the net and carried into a light-tight room, where it was opened and species were sorted under dim red light. Specimens were maintained in chilled (8°C), aerated seawater in 1-qt containers, which were placed inside light-tight boxes. All trawling was conducted between the hours of 2200 and 0500.

Table 1

Daytime depth distribution of crustaceans in this study

Species	Depth (m)*
Family Euphausiacidae	
Stylocheiron maximum	250–500 (1)
Nematobrachion sexspinosus	400–600 (1)
Nematobrachion flexipes	450–600 (1)
Family Oplophoridae	
Janicella spinacauda	500–600 (2)
Oplophorus gracilirostris	500–650 (2)
Systellaspis debilis	600–900 (2)
Family Penaeidae	
Funchalia villosa	300–500 (3)
Family Sergestidae	
Sergia filictum	600–900 (4)

* Numbers in parentheses indicate the source of the data: (1) Roger, 1978; (2) Hopkins *et al.*, 1989; (3) Hopkins *et al.*, 1994; (4) Flock and Hopkins, 1992.

Electrophysiological recordings

The species in this study ranged in size from 20 mm body length (the euphausiids and *Janicella spinacauda*) to 80 mm body length (*Oplophorus gracilirostris*). They were mounted on an acrylic plastic holder and suspended in a chilled (8°C) seawater bath with the dorsal surface of the eyes just above the level of the water. In this configuration, which allowed their pleopods to remain free to generate respiratory water currents around the gills, the crustaceans remained alive and healthy for the duration of experiments lasting up to 12 h. A tungsten microelectrode (10 μm tip; F. Haer and Co.) was placed subcorneally in the left eye. A reference electrode was placed in the right eye, which was then covered with black petroleum jelly (petroleum jelly mixed with black oil-based paint) to block all light input to this eye. This differential recording technique was used so that background noise was subtracted from the signal before amplification. A silver chloride electrode grounded the water bath. Electrodes were placed in the eyes under dim red light (>650 nm; Wratten Filter 79B). Signals were amplified with a Haer Microelectrode Amplifier (Model × Cell-3) used in conjunction with a high-impedance probe to eliminate electrode polarization artifacts (Kugel, 1977). Low-frequency filters were set to minimal filtering (0.01–0.1 Hz) to minimize distortion of the AC-amplified signal. Data were digitized using a program written in LabView (National Instruments, Inc.), and stored to disk for later analysis.

This study was conducted on shipboard because the organisms used will not survive transport to a shore-based laboratory. Due to the difficulties inherent in working on a moving and rolling vessel, only extracellular electrophysiology was possible.

Light stimuli

Test flashes of 490 nm light from an American Instruments SA monochromator (Model H-20) were delivered to the eye *via* a fused silica light guide, positioned so the circle

of light at the output was larger than the eye. A piece of lens tissue between the light guide and the eye served as a diffuser. Flash duration was controlled by a Uniblitz shutter (Model T132) under computer control, such that a 50% duty cycle (50:50 light:dark ratio) was maintained. Irradiance was controlled with a neutral-density wheel driven by a stepper motor under computer control, and calibrated with a UDT optometer (United Detector Technology Model S370) and radiometric probe with point calibrations provided by UDT.

Procedure

Although mesopelagic crustaceans are relatively insensitive to red light (Frank and Case, 1988a), the dim red preparation light did produce a small degree of light adaptation. Therefore, after electrode placement, the specimen was dark-adapted until the response to a test flash, given every 5 min, had not changed for 1 h, indicating that the eye was in its fully dark-adapted condition. A flickering light stimulus of 1.5-s duration was then presented to the dark-adapted eye. To ensure that every flicker stimulus was presented to a fully dark-adapted eye, a dim 100-ms test flash that elicited a 50-μV response (the smallest response reliably discernible from background noise) in the fully dark-adapted eye was presented to the eye after every flicker stimulus, and the eye was allowed to re-dark-adapt until the test flash response had recovered to 50 μV, before the next flicker stimulus was presented. The flicker rate for subsequent stimuli was increased until critical flicker fusion was achieved; this is defined as the point at which the eye can no longer produce a modulated electrical signal that remains in phase with the flickering light. Irradiance was then increased by one log unit, and the flicker rate of the stimulus light was increased until fusion was again achieved. Maximum critical flicker fusion frequency (CFF) is defined as the point at which further increases in irradiance do not result in a faster flicker fusion frequency. All maximum CFFs are in reference to dark-adapted eyes.

The responses to single 100-ms flashes of 490-nm light of varying irradiances were also measured, starting from irradiances generating a threshold response, and continuing to the point at which further increases in irradiance produced no further increases in response amplitude. In some preparations, the response was not saturated at the maximum stimulus light irradiance. For those preparations in which response saturation was reached, the log I_{10} was determined; this is the log of the stimulus irradiance eliciting a response that is 10% of the maximum amplitude. The log I_{10} was used as an estimate of the relative sensitivity of the photoreceptors (after de Souza and Ventura, 1989).

For all species, latencies were measured using a response amplitude that was 10% of the maximum response. Response latency is defined as the time from the start of the light stimulus to the start of the ERG.

Results

The critical flicker fusion frequency measured *via* the extracellular electroretinogram is dependent on a variety of factors, namely adaptational state, background intensity, stimulus intensity, and the subtended visual angle of the source. In this study, all factors, with the exception of the stimulus intensity, were equal for all the species: they were all completely dark-adapted before being presented with a flickering light stimulus, the background intensity was 0, and the eye was always bathed with a circle of light that was larger than the eye itself. The only variable factor was the stimulus intensity. Although the irradiance of the light source was calibrated, the response to the light stimulus depended on the position of the electrode in the eye, so that a 100-μV response might be generated by a dim stimulus in one specimen and a brighter stimulus in another specimen of the same species. As shown in Figure 1, the CFF depended on irradiance level, with lower irradiances evoking lower CFFs and higher irradiances evoking higher CFFs. Therefore, to ensure that the same parameter was measured for all species in this comparative study, the maximum CFF, which is the highest flicker rate that the eye is capable of following at any intensity, was used.

Maximum critical fusion frequency

The maximum CFFs were measured for eight species of mesopelagic crustaceans from a variety of depths (Table I).

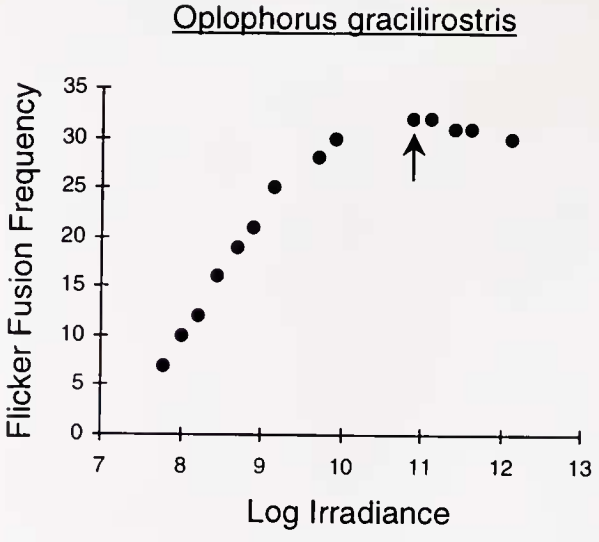

Figure 1. Flicker fusion frequency (Hz) as a function of irradiance (photons cm^{-2} s^{-1}) for *Oplophorus gracilirostris*. Flicker fusion frequency increases as the irradiance increases, up to the maximum critical flicker fusion frequency (arrow), the point at which further increases in irradiance do not result in a more rapid flicker fusion frequency.

Three species, *Sergia filictum*, *Systellaspis debilis*, and *Funchalia villosa*, had relatively low maximum CFFs, between 20 and 25 Hz (Table II), as one would expect from species coming from a very low light environment. A representative example of an ERG is shown for *Systellaspis debilis* in Figure 2A. Three species, *Oplophorus gracilirostris*, *Janicella spinacauda*, and *Stylocheiron maximum*, had somewhat higher rates, between 31 and 36 Hz; and two species, *Nematobrachion flexipes* and *Nematobrachion sexspinosus*, had extremely high CFFs, considering their dim light environment, of 44 and 57 respectively (Table II). A representative example of an ERG for *N. sexspinosus* is shown in Figure 2B.

Sensitivity

The overall sensitivity of the eye was estimated by determining the log of the irradiance (log I_{10}) required to produce a response that was 10% of the amplitude of the maximum response the eye was capable of generating. In several preparations, the maximum response was not seen, and the log I_{10} could not be determined. As shown in Table II, there is a trend towards lower sensitivity to light as the response dynamics of the eye speeds up. *Systellaspis debilis*, the species with the lowest maximum CFF, had, according to the log I_{10}, the most sensitive eye, while *N. sexspinosus*, the species with the highest maximum CFF, has the lowest sensitivity to light.

Response latency

As an indicator of the speed of transduction in the photoreceptors of the various species, latency from the start of the light stimulus to the start of the photoreceptor response was measured, using a response amplitude that was 10% of the maximum amplitude. Species with lower flicker fusion frequencies also have longer latencies, indicative of slower eyes, and species with higher flicker fusion frequencies have eyes with much faster response dynamics (Table II).

Table II

Mean values for temporal resolution (max CFF), sensitivity (Log I_{10}) and response latencies obtained from ERG data

Species	Max CFF (Hz)	Log I_{10} (photons cm^{-2} s^{-1})	Latency (ms)
Systellaspis debilis	21 (±0.6; *n* = 4)	8.9 (±0.06)	58 (±6.9)
Funchalia villosa	24 (±0.5; *n* = 2)	9.3 (±0.0)	75 (±2.0)
Sergia filictum	25 (*n* = 1)	NA	NA
Janicella spinacauda	[illegible] (±0.3; *n* = 3)	9.4 (±0.06)	49 (±3.5)
Oplophorus gracilirostris	32 (±[illegible]; *n* = 2)	9.4 (±0.09)	42 (±5.5)
Stylocheiron maximum	36 (*n* = [illegible])	10.0	42
Nematobrachion flexipes	44 (±1.0; *n* = 2)	10.2 (±0.38)	22 (±0.5)
Nematobrachion sexspinosus	56 (±2.0; *n* = 4)	10.8 (±0.18; *n* = 2)	16 (±2.5)

Species are ranked by max CFF, from lowest to highest. Standard errors and number of specimens tested are in parenthesis.

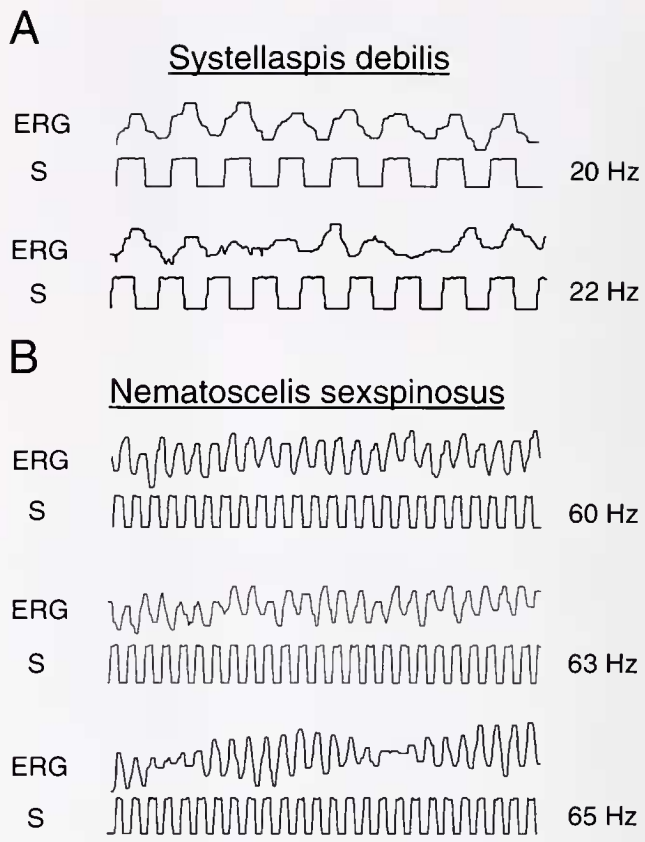

Figure 2. Representative examples of species with low and high flicker fusion frequencies. ERG designates the response recorded from the eye; S designates the flickering light stimulus. The data shown are from the last 0.4 s of the 2-s stimulus pulse. (A) The ERG from *Systellaspis debilis* was able to follow the stimulus light at 20 Hz cycle for cycle; at 22 Hz, the ERG response was lagging behind the light stimulus and "missing" cycles. (B) The ERG from *Nematoscelis sexspinosus* was able to follow the stimulus light at 60 Hz. At 63 Hz, the ERG appears to be in phase with the stimulus light, but careful examination of the data shows that 25 flashes of light were given, but only 23 responses were produced. By 65 Hz, the lag is even greater, and the ERG is clearly "missing" cycles. The CFF of this specimen is 60 Hz, since this is the last recorded frequency at which the ERG was able to match, cycle for cycle, the phase of the stimulus light.

Discussion

The vertical distributions of the species examined in this study have not been determined for the south coast of Cuba. The vertical distribution data in Table I are for the Gulf of Mexico, except for the euphausiids. Since Gulf of Mexico water originates in the Caribbean Sea (Nowlin, 1971), and both areas have Jerlov's Type 1 or 1A water (Jerlov, 1976), it is likely that these two areas would have similar species assemblages and distribution patterns. The abundance of the

three species of euphausiids in this study was extremely low in the Gulf of Mexico (Kinsey and Hopkins, 1994), as it was off the coast of Cuba (pers. obs.), and comprehensive data on depth distribution are not available for these areas. The data presented in the table are for the tropical Pacific, where Jerlov's Type 1 or 1A water is also present. The depth distributions of nine relatively abundant euphausiid species in the Gulf of Mexico (Kinsey and Hopkins, 1994) were compared with those provided by Roger (1978) for the same species in the tropical Pacific, and the depth ranges proved to be the same in the two areas. Therefore, it is likely that the data presented for the vertical distribution of *Nematobrachion flexipes, N. sexspinosus,* and *Stylocheiron maximum* in the tropical Pacific would also apply to the Gulf of Mexico.

Depth vs. critical flicker fusion

Shallower depth ranges do not necessarily mean a brighter light environment: an organism found at 300 m in murky water might see significantly less light than an organism found at 500 m in very transparent water. However, in this study, the depth of occurrence is an indication of relative light intensity, as the water is all Jerlov's Type 1 or 1A (Jerlov, 1976). Most of the species in this study live below 400 m. At 400 m during the day, in Jerlov's type 1 water, downwelling ambient light has been reduced to less than 0.0001% of the surface irradiance (Jerlov, 1976). This is about as bright as the moonlight seen by nocturnal insects, in that light from a full moon is 0.0001% of daytime illumination (Munz and McFarland, 1973; Land, 1981). Therefore, one would expect mesopelagic crustaceans to have relatively low maximum CFFs, indicative of low temporal resolution, as has been found in nocturnal insects (Autrum, 1950, 1958, 1984; Howard *et al.,* 1984; de Souza and Ventura, 1989; Laughlin and Weckström, 1993). In addition, one might expect the deepest dwelling species, which live in the dimmest light, to have the lowest maximum CFFs. This is certainly the case for the two deepest living species in this study—an oplophorid, *Systellaspis debilis,* and a sergestid, *Sergia filictum*—which have maximum CFFs of 20–25 Hz (Fig. 3), equivalent to those of the nocturnal slow moving insects studied by Autrum (1950, 1958). *Oplophorus gracilirostris* and *Janicella spinacauda* are in the same family as *S. debilis,* but have higher maximum CFFs—between 31–32 Hz. Their daytime depth range is about 100 m shallower than that of *S. debilis* (Fig. 3), so a higher maximum CFF is not unexpected. A previous study by Moeller and Case (1995) reports a critical flicker fusion frequency of 12 Hz for *Oplophorus spinosus,* which has a depth distribution similar to that of *O. gracilirostris.* However, those authors were using a light that was only 1 log unit above the irradiance that produced a threshold response, and as shown by Figure 1, a much lower critical

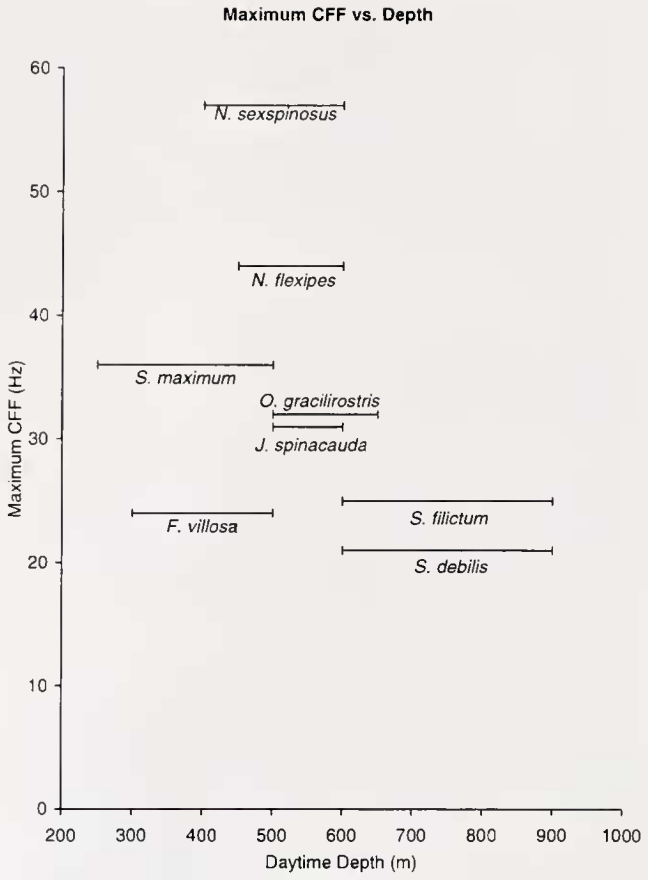

Figure 3. Maximum critical flicker fusion frequency (CFF) as a function of daytime depth distribution for the eight species in this study.

flicker fusion frequency would result from such a dim light stimulus.

At first glance, the very low maximum CFF of the penaeid, *Funchalia villosa,* is somewhat puzzling. It is one of the shallowest living species, and also possesses an eye with a fairly high spatial resolution (Herring and Roe, 1988). High spatial resolution is usually correlated with a higher light environment, and is also associated with a comparatively higher temporal resolution (Srinivasan and Bernard, 1975). However, these measurements of maximum CFF were made in a completely dark-adapted eye; the eye of *F. villosa,* which is of the superposition type, possesses migrating screening pigments, which changes the eye from a spatially acute, apposition-like eye during the day to an eye with less spatial resolution, but greater sensitivity, at night (Herring and Roe, 1988). Maximum CFF is known to be higher in the light-adapted vs. the dark-adapted eyes of shallow-water crustaceans that possess mobile screening pigments (Crozier and Wolf, 1939; Crozier *et al.,* 1939; Bröcker, 1935), but mobile screening pigments are usually not found in mesopelagic species (see Hallberg and Elofsson, 1989, for review). *F. villosa* appears to be an exception to this rule. Looking at the other species in this study, the

screening pigments in the photoreceptors of *Oplophorus spinosus* (Welsh and Chace, 1937; Land, 1976; Gaten *et al.*, 1992), a close relative of *O. gracilirostris* with the same depth distribution, and *Systellaspis debilis* (Gaten *et al.*, 1992) do not appear to be mobile. Although some species of sergestids may possess screening pigments (Welsh and Chace, 1938), it is not known whether these are mobile. Chun (1896), Zimmer (1956), and Meyer-Rochow and Walsh (1978) found no evidence of the migration of screening pigments in euphausiid eyes, and while Kampa (1965) indicates that some migration does occur, Land *et al.* (1979) conclude that this migration is not of sufficient magnitude to affect the spatial resolution of the eye. It remains to be seen whether *F. villosa*, whose spatial resolution is clearly higher when its screening pigments are in the light-adapted position, will also demonstrate a higher temporal resolution under light adaptation that is more consistent with its daytime depth distribution. Future studies will include determining the temporal resolution of *F. villosa*, as well as that of other species without migrating screening pigments, under light-adapted conditions.

The three euphausiid species in this study (*Nematobrachion sexspinosus*, *N. flexipes*, and *Stylocheiron maximum*) all have bilobed eyes, and Chun (1896) determined (morphologically) that the upper lobe, which is oriented upwards toward the brighter downwelling light, has higher spatial resolution than the lower lobe, which is oriented downwards towards dimmer upwelling light. Due to limitations set by working on shipboard, the responses from receptor cells in the upper lobe could not be isolated from responses from receptor cells in the lower lobe. Therefore, it remains to be determined whether the temporal resolution differs between the two lobes. However, it is clear that two of these species, *N. sexspinosus* and *N. flexipes*, have the highest maximum CFFs of all the species in this study, comparable to CFFs reported for shallow-water crabs (Bröcker, 1935; Crozier and Wolf, 1939). This is unexpected, because their daytime depths of occurrence are in the middle of the depth distribution for the eight species in the study (Fig. 3). These two species live at a depth at which the downwelling light intensity is roughly the same as that experienced by nocturnal insects under a full moon (see above), yet they have a substantially higher maximum CFF (40–60 Hz) than most nocturnal insects (10–20 Hz; Autrum, 1950, 1958). Laughlin and Weckstrom (1993) demonstrated that the benefits of high temporal resolution are limited for nocturnal, generally slow moving insects, and that the metabolic price for improving the temporal bandwidth of vision is substantial. In addition to the metabolic expense, fast photoreceptors have a lower sensitivity than slow photoreceptors (Laughlin, 1990), which would be a distinct disadvantage to organisms living in a light-limited environment. However, these conclusions were drawn for terrestrial organisms, and other factors must be taken into account in the oceanic realm.

Critical flicker fusion and bioluminescence

Although the crustaceans in this study share the same light regime as nocturnal insects with respect to background illumination, many of their prey are bioluminescent. Bioluminescence, which is very rare in the terrestrial environment, is an extremely common phenomenon in the oceanic realm. In the mesopelagic zone (200–900 m), luminescence has been found in up to 75% of the fish species (Herring and Morin, 1978) and 79% of the shrimp species (Herring, 1976). Nocturnal terrestrial insects must image dark objects against a dimly lit background, so a higher temporal resolution, with the resulting decrease in contrast sensitivity, would be a considerable disadvantage. In the ocean, it might be advantageous for predatory carnivorous species to sacrifice sensitivity for the ability to more accurately track a glowing or flashing prey item.

All euphausiid species with bilobed eyes possess an extremely elongated second or third thoracic leg, some with clawlike chelae at the end, which is hypothesized to be an adaptation for active carnivorous feeding (Mauchline and Fisher, 1969). If some of these species specialized in capturing bioluminescent prey, the greater contrast between a bioluminescent prey item against a dim background *vs.* a dark prey item against a dim background would make it advantageous for these species to sacrifice sensitivity (and hence contrast detection) in return for greater temporal resolution (and hence tracking ability). This rationale would likewise explain the puzzling result that *Stylocheiron maximum*, which is also a bilobed euphausiid with an elongated thoracic appendage, has the shallowest depth distribution of the three euphausiid species but also the lowest maximum CFF (Fig. 3). *S. maximum* eats primarily copepods in the genera *Oithona*, which is nonluminescent, and *Oncaea*, of which only one species is known to be bioluminescent (see Herring, 1985, for review), and this bioluminescent species is not present in the Gulf of Mexico (Kinsey and Hopkins, 1994). Since the biomass and species distribution off Cuba is similar to that of the Gulf of Mexico, it is likely that *S. maximum* is eating primarily nonbioluminescent prey in Cuban waters as well. On the other hand, the primary prey item of *N. sexspinosus* and *N. flexipes*, the two species with the highest critical flicker fusion frequencies, is an active bioluminescent copepod called *Pleuromamma* (Hu, 1978; Kinsey and Hopkins, 1994), all species of which emit some form of bioluminescent spew (see Herring, 1985, for review). To further support the argument that this visual adaptation is driven by bioluminescence, the *Nematobrachion* species, as mentioned above, have a deeper depth range than *S. maximum*, but possess a less sensitive eye, according to the log I_{10} values (Table II). Following Autrum's hypothesis, one would predict that the organism from the dimmer light regime would have the more sensitive eye with slower response dynamics (assuming similar

activity levels). However, because the *Nematobrachion* species are specializing in bioluminescent prey, the advantages of a higher temporal resolution might outweigh the advantages of a more sensitive eye.

Other species, however, might benefit from having an eye with lower temporal resolution. If the preferred bioluminescent prey were a slow moving item that glowed, such as some species of gelatinous zooplankton, or marine snow colonized by bioluminescent bacteria, an eye with a lower temporal resolution—assuming this meant a longer integration time (see below)—would actually be advantageous. This benefit would only apply to a dim "slow" signal, such as a glow or a flash with a slow rise time; a brief dim flash with a rapid rise time would be equally difficult to detect by either slow or fast photoreceptors (for a comprehensive discussion of frequency coding, see Laughlin, 1981; Laughlin and Weckström, 1993).

As stated above, the advantage of possessing an eye with a lower flicker fusion frequency depends on the assumption that a lower CFF is correlated with a longer integration time. The integration times of the eyes of the species in this study have not been measured, but de Souza and Ventura (1989) found that critical duration, another temporal characteristic of a photoreceptor that is determined electrophysiologically, is directly related to integration time, so that a long critical duration indicates a long integration time. Since the maximum CFF can be equated to the reciprocal of the critical duration (Matin, 1968), the low CFFs of most of the crustaceans in this study (the *Nematobrachion* species being the exception) indicate that they possess photoreceptors with fairly long integration times, and therefore might be well adapted for detecting dim, glowing bioluminescence. The conclusion that eyes with lower CFFs have slower response dynamics is supported by the latency data, in that the eyes with lower maximum CFFs also have longer response latencies (Table II).

In conclusion, it appears that while the mesopelagic light environment is similar to that of nocturnal insects with respect to background light, the temporal resolutions of several species found in this environment are substantially higher than would have been predicted on the basis of background light alone. In addition, the hypothesis that temporal resolution would be correlated with daytime depth distribution is not supported by these data. However, this preliminary study indicates that when bioluminescence is taken into account, Autrum's hypothesis that the response dynamics of the retina match the habitat and lifestyle of the organism appears to be valid in the oceanic realm as well as in the terrestrial environment.

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